

Short-term plasticity of the visuomotor map during grasping movements in humans

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During visually guided grasping movements, visual information is transformed into motor commands. This transformation is known as the “visuomotor map.” To investigate limitations in the short-term plasticity of the visuomotor map in normal humans, we studied the maximum grip aperture (MGA) during the reaching phase while subjects grasped objects of various sizes. The objects seen and the objects grasped were physically never the same. When a discrepancy had been introduced between the size of the visual and the grasped objects, and the subjects were fully adapted to it, they all readily interpolated and extrapolated the MGA to objects not included in training trials. In contrast, when the subjects were exposed to discrepancies that required a slope change in the visuomotor map, they were unable to adapt adequately. They instead retained a subject-specific slope of the relationship between the visual size and MGA. We conclude from these results that during reaching for grasping, normal subjects are unable to abandon a straight linear function determining the relationship between visual object size and MGA. Moreover, the plasticity of the visuomotor map is, at least in short term, constrained to allow only offset changes, that is, only “rigid shifts” are possible between the visual and motor coordinate systems.

The processes whereby sensory information is used to generate motor commands are known as “sensorimotor transformations.” Typically, they can be formalized in terms of a transformation between different coordinate systems, for instance, the “visuomotor map” transforms information from visual to motor coordinates (Pouget and Snyder 2000). Both long- and short-term plasticity of the visuomotor map has been amply demonstrated, most commonly using optical prisms that distort the visual field (cf. Welch 1978). In this study we have investigated the nature of the “constraints” that may limit the short-term plasticity of the visuomotor map, using adaptation to sensory discrepancies during grasping movements as an experimental paradigm (Säfström and Edin 2004).

It has previously been demonstrated that the maximum amplitude of grip aperture during reaching for grasping covaries with object size and that the relationship between object size and the maximum grip aperture is approximately linear (Jeannerod 1984; Marteniuk et al. 1990). The visuomotor map (f) determines the relation between visual coordinates (visual size of object, VO) and motor coordinates (maximum grip aperture, MGA) (Fig. 1A), that is, $MGA = f(VO)$. Since the relationship is linear, it can be expressed as

$$MGA = a + b \cdot VO, \quad (1)$$

where a represents the “offset” and b represents the “slope” of the relationship.

This visuomotor transformation depends on numerous factors. For instance, increased movement speed (Wing et al. 1986) and reduced lighting (Wing et al. 1986; Jakobson and Goodale 1991) affect the execution of the grasping movement and make the MGA larger, which is usually reflected as an increase in the offset (a in equation 1) and a decrease of the slope (b in equation 1). This strategy compensates for increased end-point variability of the digits during the grasp. In the present study, factors known to alter the end-point variability during execution of the grasp

were held constant (movement speed, lighting conditions, etc.) so that any change in the visuomotor map could be attributed to sensorimotor adaptation that occurred as a result of discrepancies between visual and haptic feedback about object size (Gentilucci et al. 1995; Säfström and Edin 2004).

There are no a priori limitations on possible changes in the visuomotor map: any visual coordinate could in principle be mapped onto any motor coordinate. Yet, it seems reasonable to expect constraints with respect to what maps can actually be learned: the more constraints, the less flexible is the visuomotor map. Given that the visuomotor map can be approximated by a linear mathematical function (equation 1), and the finding that the offset parameter (a in equation 1) can be modified as a result of sensorimotor adaptation (Säfström and Edin 2004), three different hypotheses about the flexibility of the visuomotor map seem to encapsulate all possible levels of constraints (Fig. 1B). These hypotheses are analogous to those proposed by Bedford (1989), who studied adaptation during pointing movements.

Minimum constraint hypothesis: Subjects can abandon the linear relationship between visual object size and MGA

If individual pairs of visual and motor coordinates are independently associated by learning, almost any visuomotor map would be possible to learn with sufficient practice. Traditionally, sensory recalibration has been compared with Pavlovian and instrumental conditioning, suggesting that individual pairs of visual and motor coordinates is the correct level of analysis (Epstein 1975). This possibility has never been tested during grasping movements. The hypothesis implies that the observed normal linear relation can be replaced by any nonlinear function or that new visuomotor maps may require individual associations between pairs of visual and motor coordinates.

Maximum constraint hypothesis: Subjects can only modify the offset parameter (a in equation 1)

We have already demonstrated in a previous study that subjects can modify the offset parameter, a (Säfström and Edin 2004). The

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Article and publication are at <http://www.learnmem.org/cgi/doi/10.1101/lm.83005>.

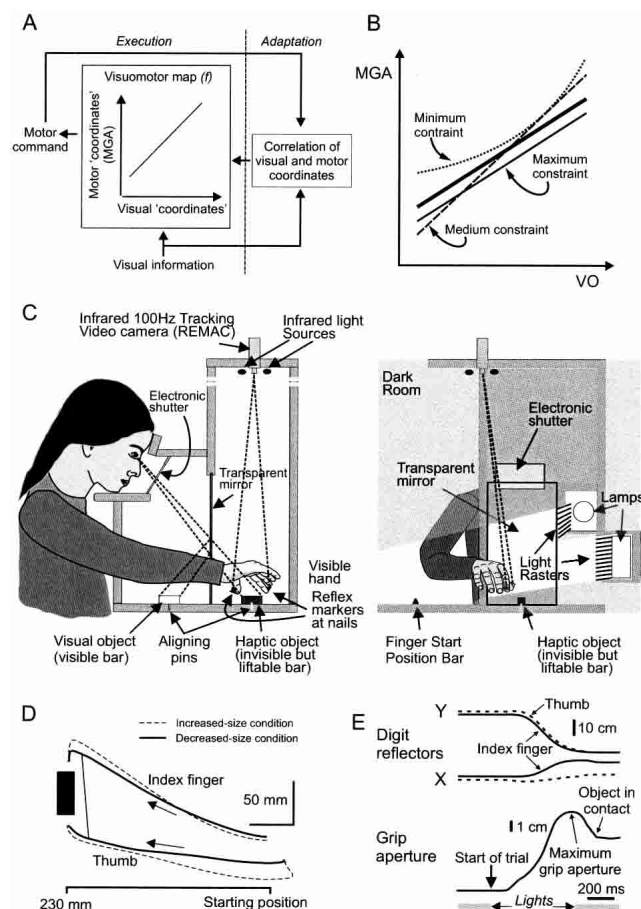


Figure 1. (A) During execution of normal grasping movements, the visuomotor map (f) determines the relation between visual coordinates (VO) and motor coordinates (MGA). This relation is assumed to be continually monitored by feedback. When a discrepancy occurs between visual and motor coordinate systems, this conflict can be resolved by means of adaptation, which implies that the visuomotor map is updated to reflect the new relation between visual and motor coordinates. (B) The normal, unmanipulated, visuomotor map is represented by the thick solid line. The dotted curved line is an example of what the visuomotor map may look like if the linear relationship is abandoned (minimum constraint hypothesis). The thin solid line represents a change in the offset parameter in the visuomotor map (maximum constraint hypothesis), and the striped line represents a change in both the offset and the slope parameter (medium constraint hypothesis). (C) A transparent mirror divided the experimental apparatus into two compartments, one with a bar visible to the subject (visible object), and one with an invisible bar that could be reached by the subject's right hand (haptic object). The haptic object was painted black and never illuminated. (D) Two single sample trajectories of the tip of the index finger and the thumb when a subject reached for a 50-mm haptic object. Both trajectories depict interpolation "test trials," one during the increased-size condition (dashed line) and the other during the decreased-size condition (thick solid line). The thin solid line indicates the maximum grip aperture for that particular trial. (E) The upper part of the picture shows the x/y coordinates for the reflex markers as a function of time, and the lower part shows how the MGA was determined in the data files (same trial as the thick solid line in D).

possibility that a is the only parameter that can be changed implies that only "rigid shifts" are possible between the visual and motor coordinate systems (i.e., that the visuomotor map can be modified only by changing the relation between visual and motor coordinates an equal amount within the entire workspace).

Medium constraint hypothesis: Subjects can modify both the offset and slope parameters (a and b , respectively, in equation 1)

An alternative hypothesis, intermediate to (1) and (2), is that the linear relation cannot be abandoned, but that both the offset and the slope can be modified. As opposed to the first hypothesis, this hypothesis implies an inherent linear constraint limiting the flexibility of possible visuomotor maps, but, as opposed to the second hypothesis, both rigid shifts and a "rescaling" may occur between the coordinate systems. This intermediate hypothesis seems plausible if the central nervous system (CNS), for instance, uses a "correlator" that simply attempts to find the best-fitting linear relation between visual and motor coordinate systems (Held 1961).

These three hypotheses were tested in two experiments (Fig. 2). In the first experiment we investigated if individual pairs of visual and motor coordinates are associated by learning (as stated by the minimum constraint hypothesis) or if there is a linear constraint when changing the visuomotor map (as stated by the maximum and medium constraint hypotheses). Subjects first made "training trials" to learn new mappings (a new relation) between isolated pairs of visual and motor coordinates. During subsequent "test trials," we investigated the subjects' performance when they encountered objects of sizes that did not appear during the training trials. If new mappings were generalized to visual objects of a size intermediate to the sizes of visual objects presented during training, the subjects would be able to "interpolate" in the visuomotor map. Similarly, they would be able to "extrapolate" if new mappings were generalized to visual objects larger or smaller than those presented during training. If the subjects were able to both interpolate and extrapolate, we would conclude that the subjects entertained a continuous function that transforms visual size into a particular grip aperture size. In contrast, if they failed to interpolate and extrapolate, we would conclude that adaptation was specific for the trained visuomotor coordinates.

In the second experiment we investigated if only offset changes are possible between the visual and motor coordinate systems (as stated by the maximum constraint hypothesis) or if a higher degree of flexibility is possible (as stated by the minimum and medium constraint hypotheses). Subjects were trained on new mappings that did not correspond to just a change in the offset. In order to learn these mappings, subjects either had to make individual associations between pairs of visual and motor coordinates (i.e., according to the minimum constraint hypothesis) or they had to make a slope change in the visuomotor map (according to the medium constraint hypothesis).

Thus, in the first experiment the maximum and medium constraint hypotheses were contrasted against the minimum constraint hypothesis, and in the second experiment the maximum constraint hypothesis was contrasted against the minimum and medium constraint hypotheses. Consequently, if one (and only one) of the proposed hypotheses is correct, then the two experiments in combination would be sufficient to decisively determine which one of them it is.

Results

Experiment 1

General grasping behavior during the equal-size condition

As expected, all subjects adjusted their maximum grip aperture to the visual size of the object during the reaching phase of the grasping movement (Fig. 3A). The relation was nearly linear for the range of object sizes presented during the first 10 trials of the

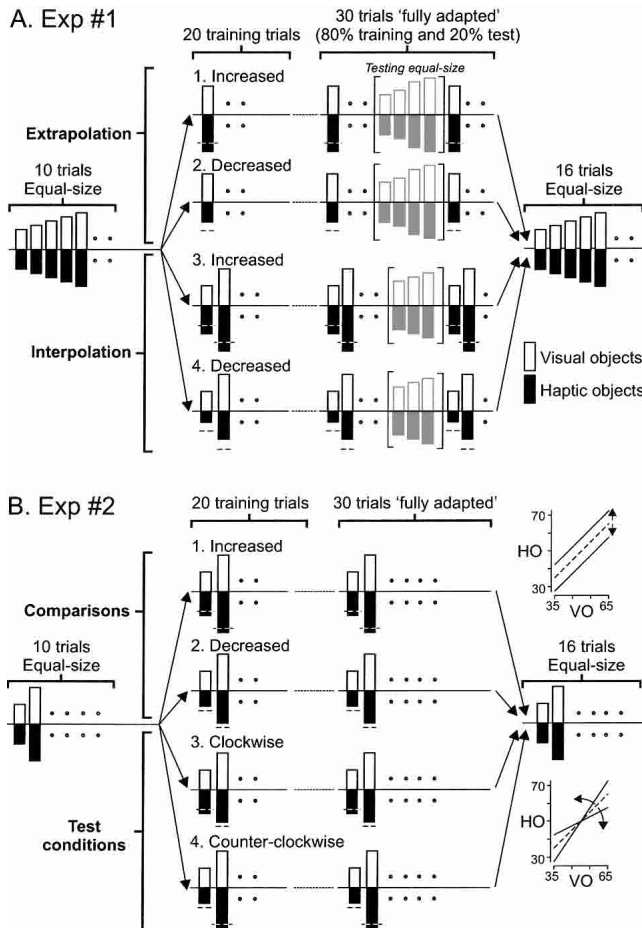


Figure 2. (A) All series in Experiment 1 started with 10 trials with equal visual and haptic object sizes of 35, 42.5, 50, 57.5, and 65 mm in an unpredictable order. Haptic and visual objects are drawn to scale and are represented by filled and open rectangles, respectively. During the following 20 training trials only one visual object (50 mm) was used in the extrapolation series and two visual objects (35 and 65 mm) in the interpolation series. The corresponding haptic object was either 15 mm larger (increased-size condition) or smaller (decreased-size condition) than the visual object (dashed lines close to haptic objects indicates the size of the visual object in the same trials). During the subsequent 30 trials every fifth trial was a test trial in which visual objects of sizes 35, 42.5, 57.5, or 65 mm were presented during the extrapolation series, and visual objects of sizes 42.5, 50, or 57.5 mm during the interpolation series. During these test trials, the visual and the haptic objects were always of equal sizes. (B) The series in Experiment 2 started with 10 trials of equal visual and haptic object size, 35 or 65 mm. In two comparison conditions, the haptic objects then became either 7.5 mm larger (increased-size condition) or smaller (decreased-size condition) than the visual objects. In two test conditions, the subjects were exposed to a “slope change” of the coordinate systems. In the clockwise slope change condition, the 35-mm visual object was associated with a larger haptic object (42.5 mm) and the 65 mm visual object was associated with a smaller haptic object (57.5 mm). In the counterclockwise slope change condition, the 35-mm visual object was associated with a smaller haptic object (27.5 mm) and the 65 mm visual object was associated with a larger haptic object (72.5 mm). In both Experiments 1 (A) and 2 (B), all analyses of the “equal-size condition” were made on the first 10 trials in each series. The first 20 trials of exposure to a size discrepancy were considered as training trials in which subjects were not fully adapted to the size discrepancy, and these trials were excluded from all analyses. During the following 30 trials the subjects were considered to be “fully adapted,” and these trials were included in the analyses. All series ended with 16 trials with equal visual and haptic object size to allow the subjects to readapt to the equal-size condition; these trials were excluded from the analyses. The *upper* and the *lower* insets illustrate “offset changes” and “slope changes,” respectively, of the visuomotor map.

experimental series (35–65 mm), with a subject-specific slope (across all subjects, 0.85 ± 0.14 , mean \pm SD) and offset (28.6 ± 11.0).

Predictions

At the 11th trial in each series, the haptic object became either 15 mm larger (increased-size condition) or 15 mm smaller (decreased-size condition) than the visual object (cf. Fig. 2A). The fully adapted behavior for the training coordinates during the increased- and decreased-size conditions averaged across subjects is illustrated in Figure 3B. The adapted values for visual objects 35 and 65 mm (circles) were retrieved from the interpolation series and the values for visual object size 50 mm (squares) from the extrapolation series.

The maximum and the medium constraint hypotheses both imply that subjects in this situation should be able to perform linear interpolation and extrapolation in the visuomotor map. Accordingly, the predicted relation between MGA and visual object size during the test trials was given by linear regression equations calculated from the fully adapted relationship during the training trials. These functions and 99% confidence intervals are depicted in Figure 3B as the “decreased-size condition” ($MGA = 27.1 + 0.78 \cdot VO$) and the “increased-size condition” ($MGA = 39.0 + 0.81 \cdot VO$), respectively.

In contrast, the minimum constraint hypothesis implies that training on isolated pairs of visual and motor coordinates induce new mappings only on these coordinates, yielding poor extrapolation and interpolation capabilities. For visual objects not encountered during training, subjects thus were expected to maintain the same relationship between visual object size and MGA as before training, that is, as during the first 10 trials of each series. Accordingly, the behavior according to the minimum constraint hypothesis could be predicted based on a linear regression analysis of the first 10 trials; this linear regression equation ($MGA = 28.6 + 0.85 \cdot VO$), and its 99% confidence intervals are depicted as “equal-size condition” in Figure 3B.

Actual mappings between visual and motor coordinates on the test trials

Figure 4 illustrates the predictions and the actual values for the test trials. The minimum constraint hypothesis obviously failed to predict the observed behavior: There was a highly significant difference between the three conditions both during interpolation (Fig. 4A) ($F_{(2,14)} = 239.2$, $p < 0.00001$) and extrapolation (Fig. 4B) ($F_{(2,14)} = 68.11$, $p < 0.00001$). There was no significant interaction between the three conditions and size of visual object, neither during interpolation ($F_{(4,28)} = 0.401$) nor extrapolation ($F_{(6,42)} = 1.263$). To further explore this issue, four different linear regression equations were calculated from the actual results during test trials. There was no significant difference between the offset values in these regressions and those predicted by the medium and maximum constraint hypotheses ($F_{(2,14)} = 2.37$, $p = 0.13$, for the decreased-size condition; and $F_{(2,14)} = 0.86$, $p = 0.44$, for the increased-size condition). The observed values were therefore not significantly different from those expected given the maximum and the medium constraint hypotheses. Thus, the subjects seemed to entertain a linear function that allowed them to adjust their MGA by means of interpolation and extrapolation. When questioned after the experiment, only three of the eight subjects were able to report that size discrepancies between the seen and the grasped objects had occurred.

Experiment 2

Grasping behavior during the equal-, increased-, and decreased-size conditions

All subjects in Experiment 2 also adjusted their maximum grip aperture to the visual size of the object during the reaching phase

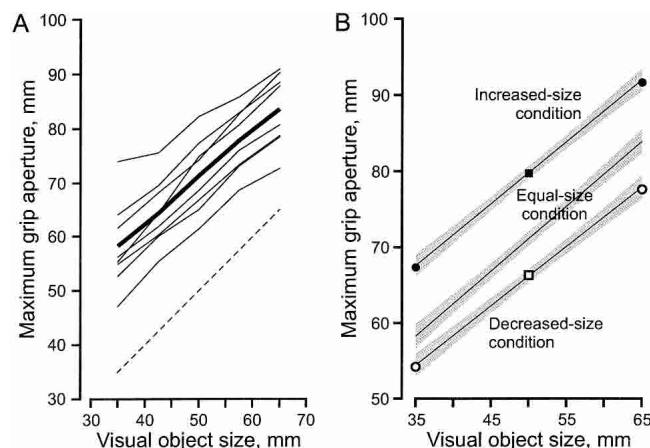


Figure 3. (A) Grasping behavior of individual subjects during the first 10 trials in Experiment 1 (thin lines). The heavy solid line represents the mean across all eight subjects. The dashed line at lower right represents the 1:1 relation between MGA and object size. (B) Data from the fully adapted behavior (averaged across subjects) for the training coordinates during the increased- and decreased-size condition was used to calculate the corresponding regression lines (the gray areas represent 99% confidence intervals). The values for visual objects 35 and 65 mm (circles) were retrieved from the interpolation series and the values for visual object size 50 mm (squares) from the extrapolation series. The regressions for the increased-size and decreased-size conditions represent the predicted behavior given the maximum and medium constraint hypotheses when subjects were adapted to the respective condition and requested to interpolate or extrapolate. Similarly, the regressions for the first 10 trials (equal-size condition) represent the predicted behavior given the minimum constraint hypothesis when the subjects were requested to interpolate or extrapolate.

of the grasping movement. The linear regression equation calculated from the first 10 trials (equal-size condition) was $MGA = 38.1 + 0.67 \cdot VO$. In the comparison series, at the 11th trial, the haptic object became either 7.5 mm larger (increased-size condition) or 7.5 mm smaller (decreased-size condition) than the visual object (cf. Fig. 2B). Linear regression equations for the fully adapted behavior were calculated for the decreased-size and the increased-size conditions and were $MGA = 37.4 + 0.64 \cdot VO$ and $MGA = 43.0 + 0.68 \cdot VO$, respectively. The linear functions for the equal-, decreased-, and increased-size conditions are depicted with dashed lines in Figure 5. Importantly noted, the estimated slopes for the three conditions were statistically similar ($F_{(2,14)} = 1.36, p = 0.29$).

Predictions

The minimum and the medium constraint hypotheses both imply that the offset and the slope parameter can be modified (cf. equation 1). Accordingly, the predictions made from the minimum and the medium constraint hypotheses were calculated by making a regression between the individual pair of visual and motor coordinates in the increased-size condition and the individual pair of visual and motor coordinates in the decreased-size condition that corresponds to that combination of pairs presented during the testing conditions. The 99% confidence intervals for these predictions are depicted as shaded areas in Figure 5A (change in slope that corresponds to a clockwise rotation) and Figure 5B (counterclockwise slope change). In contrast, the maximum constraint hypothesis implies that the offset parameter (a in equation 1) but not the slope (b in equation 1) can be modified. Given that this hypothesis predicts the slope but does not allow an exact prediction of the offset, a reasonable approach seemed to be to average the MGA in the decreased-size condition and the increased-size condition for each visual object size (note

that the magnitude and direction of any offset changes are unimportant for the evaluation of the hypothesis). The 99% confidence intervals for this prediction are depicted as the shaded area in Figure 5C (with the maximum constraint hypothesis, the same prediction applies to both clockwise and counterclockwise slope change).

Actual mappings between visual and motor coordinates in the testing series

Figure 5 illustrates the predictions and the actual behavior averaged across subjects during test trials. There was a significant main effect when comparing the two actual slopes and the three predicted slopes ($F_{(4,28)} = 27.57, p < 0.00001$). The minimum and the medium constraint hypotheses obviously failed to predict the subjects' behavior (Fig. 5A,B). A post hoc comparison of the slopes revealed a significant difference between the prediction and the actual slope both during clockwise and counterclockwise slope change (Fig. 5A,B) ($p < 0.005$ in both cases). In contrast, the actual slopes were compatible with the maximum constraint hypothesis (Fig. 5C). There was no significant difference between the slope predicted from the maximum constraint hypothesis and the actual slope during the clockwise or the counterclockwise slope change ($p > 0.97$ in both cases). Humans thus appear to be able to make offset changes ("rigid shifts") but not slope changes in the visuomotor maps during grasping movements. Only one of the eight subjects had sometimes noticed a difference in size between the seen and the grasped objects.

Discussion

We have investigated limitations in the short-term plasticity of the visuomotor map during grasping movements. In the experiments we changed the relationship between the visual size and the actual size of the grasped objects while keeping constant all other factors known to affect the visuomotor map, such as lighting conditions (Wing et al. 1986; Jakobson and Goodale 1991) and movement speed (Wing et al. 1986). In the first experiment, we demonstrated that subjects linearly interpolated and extrapolated in the visuomotor map (Fig. 4). That is, they behaved as if they used a linear function that transformed visual size into a particular grip aperture size. In the second experiment, we demonstrated that subjects maintain a specific slope even when a complete adaptation to the objects presented would require a change in the slope of the visuomotor map (Fig. 5). These results were incompatible with both the minimum and the medium constraint hypotheses but compatible with the maximum constraint hypothesis. We therefore conclude that the short-term plasticity of the visuomotor map during grasping movements is constrained in accordance with the maximum constraint hypothesis: Subjects can only modify the offset parameter (a in equation 1) of the visuomotor map, that is, only rigid shifts are possible between the visual and motor coordinate systems.

Experimental paradigm and predictions

Our experimental paradigm was used to examine the constraints that limit the plasticity of the "sensorimotor transformation," which in this study has been given the more specific denotation "visuomotor map." As such, the concept "visuomotor map" refers to the function, f , which transforms information about object size in visual coordinates (VO) into motor coordinates (MGA). "Visual coordinates" refers to the different values of object size depicted on the abscissas in Figures 3–5. "Motor coordinates" refer to the different values of the maximum grip aperture depicted on the ordinates in the same figures. Our conceptual framework implicates that changes in f represent changes in the mapping between visual and motor coordinates. In our experi-

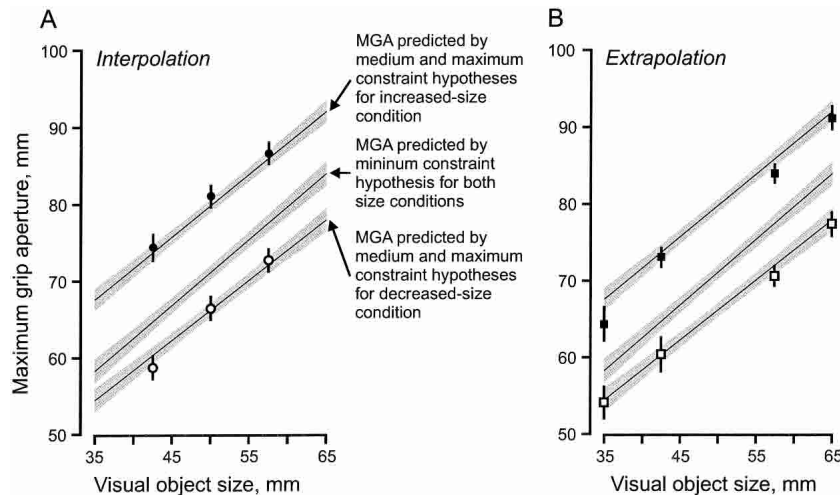


Figure 4. Actual behavior when subjects were requested to interpolate (A) or extrapolate (B). For interpolation (A), the subjects trained on visual objects 35 and 65 mm and tested on intermediate objects. For extrapolation (B), the subjects trained on the visual object 50 mm and tested on objects larger and smaller than 50 mm. The minimum constraint hypothesis failed to predict the subjects behavior whether they were requested to interpolate or extrapolate. In contrast, the observed behavior was compatible with the maximum and medium constraint hypotheses.

ments, these changes were due to sensorimotor adaptation, since other factors influencing the execution of grasping movements (e.g., movement speed and lighting conditions) were held constant. Indeed, in a previous study in which a similar experimental paradigm was used, the effects exerted on the MGA showed the cardinal features of adaptation: A behavioral reduction of effect during exposure to a discrepancy and a negative aftereffect when the normal relationship was restored (Säfström and Edin 2004).

This paradigm is not dependent on any elaborate hypothesis about how the adaptation process is accomplished, for instance, if “proprioceptive information about the hand is recalibrated by vision,” if “processing of visual information is changed,” or if adaptation is due to “visuo-motor learning” (Clower and Boussaoud 2000; Baraduc and Wolpert 2002). Our interpretation of adaptation as a change in the mapping between visual and motor coordinates is compatible with all these hypotheses, since potential answers to these suggestions lack operational definitions within our experimental paradigm.

Although the MGA varied linearly with object size (see Fig. 3) in accordance with previous studies (e.g., Marteniuk et al. 1990), the MGA is not a direct measure of the perceived size of the object as a subject would report it in a perceptual task. Rather, the “action system” uses information about an object in visual coordinates to construct a motor command, and this motor command is expressed in motor coordinates (Colby and Goldberg 1999). The MGA is in this experimental paradigm used to quantify the motor command, that is, since the MGA is a parameter of the prehensile act that is well correlated with object size, it is used to enable a mathematical description of how information about the object in visual coordinates is transformed to motor coordinates.

Subjects made 50 trials during exposure to a size discrepancy in the experimental series (Fig. 2). Previous studies have demonstrated that it takes <20 trials to adapt to a discrepancy in size between visual and motor coordinates during grasping movements (Säfström and Edin 2004). The possibility remains, however, that longer adaptation periods would enable subjects to adapt to visuomotor rearrangements to which they cannot adapt during the 50 trial periods used in our experiments. Indeed, it has been suggested that humans are capable to adapt to almost any imaginable rearrangement of vision (Welch 1978). Therefore, the results obtained in this study cannot be generalized beyond the scope of short-term adaptation.

The predictions we derived from the three proposed hypotheses require some discussion. It seems obvious that the maximum constraint hypothesis predicts that new mappings learned during training will be linearly inter- and extrapolated during the test trials as depicted in Figure 4 and also that the medium constraint hypothesis renders this prediction for interpolation performance (Fig. 4A). However, it is not evident that the medium constraint hypothesis renders the prediction about extrapolation depicted in Figure 4B, because this prediction presupposes that the slope will not change compared to the initial 10 trials. Given the assumption that the slope did not change, this outcome is, however, clearly compatible with the medium constraint hypothesis, even though a linear extrapolation with a different slope would also be compatible with this hypothesis. The predictions from the minimum constraint hypothesis depicted in Figure 4 are the result of a “pure” interpretation of this hypothesis, because the prediction states that no effect of the new mappings acquired during the

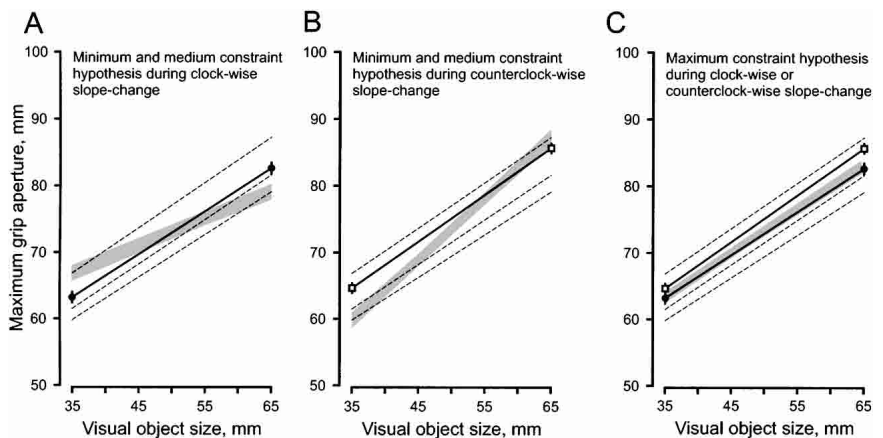


Figure 5. Actual and predicted behavior when subjects were requested to change the slope of the visuomotor map. Dashed lines represent the linear regression equations calculated from the first 10 trials of the experimental series and from the fully adapted behavior during the decreased- and increased-size conditions (notice that the haptic objects differed from the visual objects by 7.5 mm, not 15 mm as in Figs. 3 and 4). The gray areas represent 99% confidence intervals for the predictions given the minimum and medium constraint hypotheses (A, B), and the maximum constraint hypothesis (C). Filled circles represent the mean of actual maximum grip aperture (MGA) during clockwise slope change, and open squares represent the actual mean of MGA during counterclockwise slope change. The slopes predicted by the minimum and medium constraint hypotheses were significantly different from those observed (A, B), while this was not the case for the slope predicted by the maximum constraint hypothesis (C).

training trials will be found during the test trials. However, alternative predictions are possible assuming a less strict interpretation of this hypothesis. Without abandoning the hypothesis, one could expect that nearby coordinates are also likely to be affected by training, but that the effect of training will decrease as the distance increases from the trained coordinate. This would be comparable to the generalization gradients found in typical conditioning experiments. Although such a moderate prediction seems reasonable, no generalization gradients were found in our data (there was no significant interaction between conditions, neither during interpolation nor extrapolation). According to another less strict version of the minimum constraint hypothesis, subjects associate individual pairs of stimuli and response, but are still able to perform linear interpolation between these pairs (Koh and Meyer 1991). This version cannot, however, account for the observed extrapolation behavior.

Regarding Experiment 2, because the maximum constraint hypothesis does not specify the direction or magnitude of any change in offset that may occur during the testing series in this experiment, the prediction depicted in Figure 5C reflects an assumption that the offset value during the testing series will be the average of the offset values across the increased- and decreased-size conditions. This prediction is, however, clearly compatible with the maximum constraint hypothesis, whereas it is not compatible with any of the other hypotheses. The predictions based on the minimum constraint hypothesis and the medium constraint hypothesis depicted in Figure 5, A and B, represent pure versions of these hypotheses, because the predictions state that changes in slope will completely accommodate the slope changes between visual and motor coordinates presented during the testing series. "Completely accommodate" means that the relation between visual object size and MGA for a specific pair of visual and haptic objects during the testing series would be the same as the relation for that pair of objects during the comparison series. Without abandoning the hypotheses, one could, however, predict that the slope will merely change during the testing series to accommodate the slope changes. Nevertheless, since there was no significant difference when comparing the slope predicted from the maximum constraint hypothesis with either of the actual slopes (Fig. 5C), that is, no change in the slope occurred, our data do not support even these more moderate predictions.

A relatively large discrepancy between objects (15 mm) was used in Experiment 1 since we wanted to enhance the sensitivity of the experiment in detecting interactions between conditions that may have occurred because of any generalization gradient. That despite this, only about one-third of the subjects became aware of the size discrepancy is in line with a previous study, where it was also demonstrated that conscious awareness of incongruities between visual and haptic information did not influence sensorimotor adaptation during grasping movements (Säfström and Edin 2004). In Experiment 2, a smaller discrepancy (7.5 mm) was used because the different visual object sizes in this experiment would otherwise have corresponded to the same haptic object during clockwise slope change.

Interpolation and extrapolation during sensorimotor and cognitive tasks

Interpolation and extrapolation behavior has previously been investigated in tasks involving sensorimotor discrepancies. Two different kinds of generalization during such tasks can be distinguished.

First, the capacity to inter- and extrapolate sensorimotor mappings to other coordinates within the workspace reflects generalization "within sensory dimensions." It has previously been

examined whether the adaptation observed when making pointing movements during exposure to a visuomotor shift reflects a new relation between individual pairs of inputs and outputs, or represents a new relation between whole dimensions of stimuli and response. It appears as if training at individual coordinates generalizes to untrained coordinates and that there is an inherent linear constraint on the mapping between sensory dimensions (Bedford 1989, 1993; Vetter et al. 1999). These results are compatible with ours in the sense that they reject the minimum constraint hypothesis. It seems plausible, however, that different levels of constraints may be used for different visuomotor maps. Indeed, in a pointing task, Bedford (1989) found that the slope could be changed, a finding that is compatible with the medium constraint hypothesis rather than the maximum constraint hypothesis corroborated by our results.

Second, generalization of sensorimotor maps "between different movements" may occur. However, a change in the sensorimotor map that has been learned for a movement with particular dynamics and kinematics does not seem to generalize substantially to movements with other dynamics or kinematics. For instance, adaptation does not convey between fast and slow movements (Kitazawa et al. 1997), different remappings are obtained for different starting locations (Ghahramani and Wolpert 1997) and different starting postures (Baraduc and Wolpert 2002) of the arm when making pointing movements, and adaptation when making overhand throws does not generalize to underhand throws (Martin et al. 1996). The results obtained in those studies indicate that changes in the visuomotor map do not affect the visuomotor map for movements with other dynamics or kinematics. It is therefore unlikely that the change in the visuomotor map that we observed would affect other kinds of movements.

Interpolation and extrapolation capabilities have also been investigated in cognitive tasks involving function learning. A characteristic such experiment implies that subjects are trained to associate individual pairs of stimuli and response, such as temporal duration and spatial extent (Koh and Meyer 1991), or the lengths of horizontal bars (DeLosh et al. 1997; Bott and Heit 2004). The subjects are then tested on stimuli not encountered during training. These studies suggest that many cognitive behaviors are not dependent on associations between just individual pairs of inputs and outputs, but represent the learning of a relation that connects whole dimensions of stimuli and response. As such, function learning experiments have revealed a latent capacity to both interpolate (Koh and Meyer 1991) and extrapolate (DeLosh et al. 1997) previous knowledge. It was recently demonstrated that subjects are capable of extrapolating in a sinusoidal manner when such a response is required (Bott and Heit 2004). These data are encapsulated by the minimum constraint hypothesis, suggesting a low level of constraints on extrapolation behavior during cognitive tasks. In fact, when constraints on cognitive and sensorimotor learning were compared in a task that investigated the capacity to learn new relations between positions in proprioceptive and visual space, it was found that cognitive learning was more flexible than sensorimotor learning (Bedford 1993).

The functional advantage of a "maximum constraint" on the flexibility of visuomotor maps during grasping

It thus seems as if interpolation and extrapolation is a general ability used in both motor and cognitive tasks. In a recent study, it was demonstrated that the computational challenge that inter- and extrapolation poses for the nervous system can be solved by linear collective computation and least-squares error learning be-

tween populations of monotonically tuned neurons (Guigon and Baraduc 2002). A plausible teleological explanation as to why biological systems have developed such an ability is that they often must generate suitable behavioral responses based on incomplete earlier experience. This ability is fundamental for many motor and cognitive behaviors and entails that previously obtained experience can be generalized to situations not encountered before.

Teleological considerations may also elucidate why varying levels of constraints are used by different sensorimotor and cognitive systems. As emphasized by Bedford (1993), a low level of constraints is advantageous in the sense that it permits highly flexible mappings. This may be important when the relation between stimuli and response is nonlinear and complex. In contrast, a higher level of constraints has the benefit of making the generalization process faster and more efficient: To learn a relationship between visual and motor coordinates as a function requires less training than if the relationship has to be learned separately for each individual coordinate pair. That seems to disqualify the minimum constraint hypothesis as an advantageous strategy for updating visuomotor maps, because the relation between visual and motor coordinates often seems to be easily described by linear functions. Furthermore, changes in the visuomotor map during grasping can usually be represented by rigid shifts: It is, for instance, hard to imagine a real situation where some objects appear smaller whereas others appear larger. If slope changes, therefore, seldom are required, a maximum constraint may be preferred instead of a medium constraint. Indeed, if information is very scarce (that is, only one data point), only a maximum constraint can facilitate extrapolation. It, therefore, seems reasonable to assume that it is functionally advantageous to have a "maximum constraint" on the short-term flexibility of visuomotor maps during grasping. A maximum constraint may maximally facilitate the capacity to generalize incomplete prior experience, and therefore enhance the ability to behave appropriately in new situations.

Materials and Methods

Subjects

Eight right-handed subjects (3 men; 5 women; ages 18–28) participated in Experiment 1 and eight other right-handed subjects (4 men; 4 women; ages 19–28) participated in Experiment 2. The subjects were naive to the purpose of the experiment and had no impairments in their motor functioning. The experimental procedure was approved by the local Ethics Committee of the Faculty of Medicine, Umeå University. All subjects gave their informed, written consent prior to the experiment in accordance with the declaration of Helsinki.

Apparatus and procedure

The apparatus and general procedure have been described in detail previously (Säfström and Edin 2004). In short, a transparent mirror divided the experimental apparatus into two compartments, one with an object reflected in the mirror and visible to the subject (visual object), and one with an invisible object (haptic object) that could be reached by the subject's right hand (Fig. 1C). The visible object was located in spatial correspondence with the haptic object, making the subjects falsely believe they were seeing and grasping the same object. A trial started when an electronic shutter opened and lamps simultaneously switched on. Subjects were instructed to grasp, lift, and put down the object and then return the hand to a fixed starting position at their own chosen pace. The hand was illuminated during the transport of the hand toward the haptic object, but the shutter closed and the lamps switched off when the distance between the finger tips and the long axis of the object became <20 mm. The experimenter changed objects between trials and started a new

trial by pressing a button. Reflex markers were attached to the thumb and index finger (Fig. 1C). The position of the markers was recorded by an infrared 100 Hz tracking video camera (Sandström et al. 1996), and fed to a digital sampling system (SC/ZOOM) for off-line processing and analysis (Fig. 1D,E). To determine if the subjects had noticed any size discrepancies between the visual and haptic objects, the subjects were asked immediately after the experiment if they had noticed anything peculiar when grasping the objects, and if so, what.

Experimental design

Each experiment consisted of four different series of trials (illustrated in Fig. 2).

Experiment 1 (Fig. 2A)

All experimental series started with 10 trials with equal visual and haptic object size (equal-size condition). During these trials five different object sizes (35, 42.5, 50, 57.5, and 65 mm) were presented to the subjects. The purpose of these trials was to examine the normal, "unmanipulated" relationship between object size and the subject's maximum grip aperture. The initial 10 trials were followed by a period of 20 training trials in which only one visual object (50 mm) was used in the extrapolation series and two visual objects (35 and 65 mm) were used in the interpolation series. The corresponding haptic object was either 15 mm larger (increased-size condition) or smaller (decreased-size condition) than the visual object. The purpose of these trials was to introduce new mappings for one or two isolated pairs of visual and motor coordinates. After that followed a period of 30 trials in which training trials were mixed with test trials that occurred every fifth trial. During the test trials, visual objects of sizes 35, 42.5, 57.5, or 65 mm were presented during the extrapolation series and visual objects of sizes 42.5, 50, or 57.5 mm during the interpolation series. The sizes were presented in a mixed order, but distributed across series such that each object size was presented an equal number of times. During the test trials, the visual and the corresponding haptic object were always of the same size. The purpose of these trials was to study the subject's ability to extra- and interpolate to untrained visual coordinates. All experimental series ended with 16 trials with equal visual and haptic object size, giving the subjects an opportunity to readapt before the start of the next series.

Experiment 2 (Fig. 2B)

All experimental series started with 10 trials with equal visual and haptic object size (equal-size condition). During these trials two different object sizes were used (35 and 65 mm). In two test conditions the subjects were exposed to visual and haptic objects that correspond to a "slope change" of the coordinate systems; in the first test condition, one visual object (35 mm) was associated with a larger haptic object (42.5 mm) and one visual object (65 mm) was associated with a smaller haptic object (57.5 mm) (clockwise slope change); in the second test condition, one visual object (35 mm) was associated with a smaller haptic object (27.5 mm) and one visual object (65 mm) was associated with a larger haptic object (72.5 mm) (counterclockwise slope change). In two comparison conditions, a pure "offset change" of the coordinate system was accomplished by presenting haptic objects that were either 7.5 mm larger (increased-size condition) or smaller (decreased-size condition) than the two visual objects (35 and 65 mm). The exposure period to each of the four conditions consisted of 50 trials. Finally, all experimental series ended with 16 trials with equal visual and haptic object size to enable readaptation before the next series.

In both experiments, all subjects made the same set of trials and thus participated in all conditions. Each of the four series consisted of 76 trials and each series was run twice making the total number of trials in each experiment: 4 series \times 76 trials \times 2 runs = 608. The series were presented in a counterbalanced order between subjects, so that each series was presented an equal number of times on every position in the ordering of

series during an experimental session. The total time for one experimental session was ~2 h.

Data processing and statistics

In addition to the MGA, other parameters of the prehensile movement were measured: The tangential velocity for an imaginary point centered between the digits at the time of MGA, the distance from this point to the center of the object at the moment of MGA, the time from the movement start until MGA, and the time from MGA to contact with the object. The maximum achievable grip aperture, that is, the maximum distance between the index finger and the thumb, was also measured in all subjects. The analyses of these parameters did not contribute any interesting results concerning the topics addressed in this study. The MGA was recalculated to represent the maximum distance between the fingerpads, not the distance between the reflectors.

In a small number of trials (3.6% in Experiment 1 and 2.8% in Experiment 2) it was not possible to identify a clear peak in the distance between the index finger and the thumb (cf. Fig. 1D). These trials were excluded from the analyses. Previous studies have demonstrated that subjects gradually adapt to a size discrepancy and that it takes <20 trials to become fully adapted, that is, after 20 trials subjects have developed a new stable relationship between the MGA and the visual size of the object (Säfström and Edin 2004). Therefore, the first 20 training trials were excluded from all analyses and the fully adapted behavior was represented by the following 30 trials. The predictions calculated in the experiments were determined by fitting linear equations to the corresponding data using least-squares regression. During these analyses, 99% confidence intervals for the fittings were also calculated.

In Experiment 1 the differences between conditions in MGA for test trials were analyzed in two different repeated measures ANOVA, one for extrapolation behavior: 3 (condition: decreased, equal, and increased) \times 4 (size of visual object: 35, 42.5, 57.5, and 65 mm), and one for interpolation behavior: 3 (condition: decreased, equal, and increased) \times 3 (size of visual object: 42.5, 50, and 57.5 mm). The differences in offset between test trials and the prediction from the medium and maximum constraint hypotheses were analyzed in two single-factor repeated measures ANOVA, one for the decreased- and one for the increased-size condition. In each of these analyses three different offsets entered: extrapolation and interpolation test trials and the prediction. In Experiment 2 the differences between the slopes during the equal-, increased-, and decreased-size conditions was tested in a single-factor repeated measures ANOVA. The difference between the actual slope values during clockwise and counterclockwise slope change and the slope values predicted by the hypotheses was also analyzed in a single-factor repeated measures ANOVA, where all these five slopes entered. Four different post hoc comparisons were made: The actual slopes during clockwise and counterclockwise slope change, respectively, were compared with the corresponding prediction made from the minimum and medium constraint hypotheses and the prediction made from the maximum constraint hypothesis. The results of the post hoc comparisons were corrected for cumulative Type I errors with the Scheffé test. For both experiments, a significance level of 0.05 was chosen.

Acknowledgments

This work was supported by grants from the Swedish Medical Research Council (project 08667), the 5th Framework Program of

EU (projects: QLG3-CT-1999-00448 and IST-2001-33073), and the 6th Framework Program of EU (IST-001917). We thank Göran Westling for constructing the experimental apparatus and Anders Bäckström for computer support.

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Received March 1, 2004; accepted in revised form November 12, 2004.